The Meaning of Stability

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To many ecologists their science has seemed to undergo a major transformation in the last 10 years, from a qualitative and descriptive science to a quantitative and theoretical one. Yet the seminal works of mathematical ecology were written by Lotka and by Volterra more than 40 years ago, and we have barely progressed beyond them. To others, the change has seemed to be from a static to an evolutionary view of ecology, yet it is 60 years since Clements began constructing the theory of succession, which is nothing if it is not an evolutionary theory of the community. Yet there *has* been a change in ecological theory in recent years, as a glance at the pages of *The American Naturalist,* or even of *Ecology,* will show. In my view, the change has come about through a union of these two strains – the mathematical and the evolutionary – to produce the beginning, and only the bare beginning, of an exact theory of the evolution of communities of organisms. Such an exact theory must "explain" in some sense the present state of the biosphere, but must also contain statements about the past history of living communities and about their future as well. Indeed, their present state can be regarded as only a snapshot, catching at one instant of time the instantaneous configuration of an ever-shifting system.

To carry out such an ambitious program as the modern ecologist has planned requires a general abstract frame on which an exact theory can be constructed, and it is not surprising that this frame turns out to be, for ecology in general, the same as that for the specialized branch of ecology called population genetics, that is, *the concept of the vector field in* n*-dimensional space.* This concept is the most fundamental one we have for dealing with the transformations of complicated dynamical systems in time. It comes to ecology and population genetics in large part from physics, by analogizing the changes through time of a population or community with the changes in the position of a particle in space, or, on a more generalized level, with the position of a population of particles in a phase space.

THE DYNAMICAL SPACE

For any physical system we can construct a description that is a list of the variables necessary to specify the system completely plus a list of the values of those variables taken for some specific case. For example, for the purposes of guiding a space capsule to the moon it is necessary and sufficient to know, at any instant, the three coordinates of the capsule in physical space, the three components of velocity, and the three components of acceleration along these (or other orthogonal) axes. The components of acceleration result partly from the rocket power given to the capsule and partly from the combined gravitational field of all celestial bodies, but that does not complicate the space. Thus the space capsule moves or "evolves" in a "space" of 9 dimensions. The 9 dimensions may be x, y, and z coordinates of a Cartesian system with velocity and acceleration along the same axes, or some other set of orthogonal axes as, for example, distance from the center of the earth, azimuth, and altitude angles, together with velocity and acceleration values.

The total history of such an object can be described as the succession of positions of the object in the n-dimensional hyperspace of its description. The n-dimensional description we will call a *position vector*. A complete theory of evolution of the position vector would then be a set of rules relating the position of the point in hyperspace at one instant to its position at some other instant. It is the set of rules that determines the dimensionality of the space. For example, it is impossible to specify the position of a space capsule at some future time only from a knowledge of its present position. The components of velocity and acceleration are both also required because the laws of motion contain them. The rules of transformation specify, for every point in the hyperspace, the direction in which an object in the space would move at that point and the magnitude of the motion. We may imagine that at each point in the space there is an arrow pointing in some direction and having a length proportional to the magnitude of change. Such an arrow is a *transformation vector,* and the space of these vectors is a *vector field.* If we could visualize such a vector field and if it were nicely behaved, we could trace out the path that a particle would take in the space. When we sprinkle iron filings on a sheet of paper over a magnet we are visualizing the vector field for a small dipole moving under the influence of the magnet.

If the dimensions of the dynamical space have been properly chosen, there will be one and only one vector at each point and there will be a proper vector field. This is equivalent to saying that trajectories traced out by the vector field never cross. For if they crossed, then at the point of crossing there would be an ambiguity. Such an ambiguity means that all the information necessary for specifying the direction and rate of change is not contained in the coordinates of the point. Thus the dimensions used to construct the hyperspace are not sufficient to describe completely changes in the dynamical system. We will say that a set of dimensions is *sufficient* if paths in a hyperspace constructed from that set of dimensions never cross. We will then define the dimensionality of a dynamical system as the smallest number of dimensions making a sufficient set.

The rules, then, make the vector field of transformation and thus determine the configuration of the space in which the particle moves. If we are to see clearly what is meant by stability in ecology, it is essential that we differentiate between this vector field and its properties, on the one hand, and the objects – individuals, populations, species – that move in it, on the other. That is, we must distinguish between the configuration of the hyperspace in which the community is moving and the actual trajectory of the community. This distinction has not always been made. As we will see, constancy of the position vector does not imply stability in the field of transformation vectors.

STATIONARY, TRANSIENT, AND CYCLIC POINTS

In the hyperspace of the dynamical system we must distinguish three sets of points. The first is the set of points at which the magnitude of the transformation vector is zero. This is the set of *stationary points* of the system. If the position vector takes one of these values, the system does not change. *Transient points* of the space are those for which the transformation vector lengths are non-zero so that the system will continue to evolve through them. We must distinguish between cyclic and noncyclic transient points. Cyclic transient points are those to which the object may return over and over again because the configuration of the vector field causes the position vector to follow a closed path through the space. Finally, a noncyclic transient point is one through which the system would pass less than infinitely often. Any particular dynamical hyperspace may contain no, one, or more than one point falling into each of these classes, and it is the locations of these points and their numbers that determine the qualitative nature of the evolutionary system.

NEIGHBORHOOD STABILITY

Consider the nature of the vector field very near a stationary point. Do all the vectors point toward the stationary point? If they do, then it is a *stable* point, since a small perturbation of the system will result in the system returning to that point. It is necessary to specify that the perturbation is *small* because there may be several such stable or attractive points in the space and each will have its own *basin of attraction*. If the perturbation is sufficiently large to carry the system out of one basin of attraction into another, the original point is still a stable point even though the system did not return to it. Here again we must distinguish between the behavior of the position vector and the configuration of the vector field of transformation vectors. We may put this in a different way. Let $[v^*]$ be the position vector at the stationary point and $[v]$ be the position vector at some other point. Let T be the transformation that transforms $[v]$ in some unit of time. Then

$$[v(t+1)]=T[v(t)] \tag{1}$$

and

$$[v(t+n)]=T^{(n)}[v(t)]\,. \tag{2}$$

The question is, does

$$T^{(n)}[v(t)]\rightarrow[v^*] \tag{3}$$

as n goes to infinity, and, if so, for what set of $[v]$? The set of $[v]$ for which (3) is true defines the basin of attraction of $[v^*]$. In general, this is a very difficult mathematical problem. The usual approach is that of Lyapunov, which is to examine $[v]$ only arbitrarily close to $[v^*]$, that is, in the neighborhood of the equilibrium. Then, for a large class of transformations, those that converge when expanded in a Taylor series, the transformation, T, is arbitrarily close to a linear transformation **L**. If we now set

$$[x]=[v]-[v^*] \tag{4}$$

so that $[x]$ is the vector of deviations of the system from the equilibrium point $[v^*]$, we can write the dynamical equation (1) as

$$[x(\mathrm{t}+1)]=\mathbf{L}[x(\mathrm{t})] \tag{5}$$

where $\mathbf{L}-\mathbf{I}$ is the matrix of partial derivatives of the system T with respect to the components of the vector $[v]$, evaluated at $[v^*]$. The problem of stability is, then, does

$$[x(t+n)] \rightarrow 0 \qquad (6)$$

as n goes to infinity?

The behavior of $[x(t+n)]$ in the limit is determined by the characteristics of the matrix L and in particular by the eigenvalues of that matrix. If all the eigenvalues, λ_i, have their real parts less than unity, the equilibrium is stable. If any of the eigenvalues have real parts greater than unity, then the equilibrium is unstable to perturbations in some directions. That is, the transformation vectors point toward the equilibrium from some directions and away from it in others. Presumably no natural system can remain at such an unstable point, since perturbations in the wrong direction are certain to occur by chance. Finally, if the roots are complex with real parts equal to unity, the point in question is a cyclic point, part of a cyclic path. The classical prey-predator model of Lotka and Volterra is an example of a system in which the eigenvalues of L are of this form so that the prey and predator species both undergo a cyclic oscillation in numbers. These oscillations can be represented in our general framework as a closed path in a plane whose two dimensions are N_1 and N_2, the number of prey and the number of predators.

Neighborhood stability or "Lyapunov stability" is the one best understood and easiest to test for, because it is mathematically most tractable. By assuming that we will examine the vector field *arbitrarily close* to the equilibrium point, we are allowed to make nonlinear processes into linear ones that have a unique solution. Simple rules for testing stability can be derived by using the eigenvalues of the matrix L. Many authors have considered this kind of stability for population problems, for example, Lotka[1,2] and Leslie[3,4] for population growth. Especially in population genetics, where stability has been a preoccupation for a long while, Lyapunov stability is part of the standard repertoire of all theoreticians and appears explicitly or implicitly in every paper on the subject of equilibria.

GLOBAL STABILITY

The trouble with neighborhood stability is precisely that it is a simple yes or no test for the behavior of a system *at a point,* i.e., for arbitrarily small perturbations. But how will the system behave for large perturbations? If the system is far away from a stable equilibrium point, will it go toward that point or toward some quite different one? This is the question of the size and configuration of the domain of attraction of an equilibrium. It is a difficult and in large part unsolved problem, and no neat solution such as the size of the largest eigenvalue of some matrix can be invoked. Wider considerations of stability require the introduction of other concepts, some of which are as yet unexplored mathematically, but if a realistic view of the stability of ecological systems is to be obtained such new concepts and techniques are needed.

The first concept to be considered is the well-known notion of *global* stability. A locally stable point is said to be globally stable if the system converges to that point from all other points in the space. This global stability is a negative condition in that a point is globally stable only if no other point in the space is a stable point or a cyclic point. To test for the global stability of a point then involves showing that there are no other stable points, and this in turn may be trivially easy or impossibly difficult.

If the system of equations describing the transformation is linear, there can be only one equilibrium point for which all the components of the position vector are nonzero. Thus, if there is a locally stable point of this type, it must also be globally stable. However, there may also be other stable equilibria in which one or more of the components is zero, and each of these would be globally stable within the restriction that only that set of components could be zero. This points out that global stability must be defined in terms of the universe of interest. If we are interested only in that part of the space not including the margins where some of the position vector components are zero, then a linear system can have only one stable point and it will be globally stable. But if we are interested also in missing components, then even a linear system is not restricted to a single stable point.

One of the most interesting problems of community ecology comes under this rubric. Can there be more than one stable community composition in a given habitat? In our terms we are asking whether, in an n-dimensional space of the numbers of n different species, there can be more than one locally stable point. If the system of equations governing the species composition of the community is linear, then only one stable composition is possible with *all the species represented*. However, there may be other stable points with some of the species missing. Thus a given set of species abundances might be globally stable given the restriction of a certain taxonomic diversity, but not globally stable if lower taxonomic diversity is allowed. Moreover, we may state a converse proposition. If a given set of species has no locally stable point, those species cannot be made to coexist stably by adding another species. That is, if there is no locally stable point in n dimensions (not including the boundaries) there is no locally stable point in any $n+k$ dimensions within which those n dimensions are embedded.

If the system of equations describing the transformation of state is nonlinear, nothing of the foregoing holds. There may be multiple stable points with all species present so that local stability does not imply global stability. Moreover species that cannot coexist can be made stable by a third species. Man is the third species in many cases. He stabilizes unstable species composition by making nonlinear adjustments in the species abundances. In general, a study of local stability does not give information about global stability, and an analysis involving exclusion of other stable points is necessary.

DISSIPATION AND STABILITY

In the physical systems, the change of state is often described in terms of the change in the level of energy. In classical mechanics a system will move to a point of (locally) minimum potential energy, and the evolution of the system can be described in terms of the dissipation of energy. In general, at time t there is an energy function $W(t)$ such that

$$W(t+k) \leqslant W(t) \tag{7}$$

for all t and k. The equality in (7) holds only at equilibrium, and for all transient states of the system the function W is always decreasing in time. This energy function is sometimes called a Lyapunov function, and, at a point showing Lyapunov stability, the Lyapunov function is at a local minimum. We must emphasize a *local* minimum however, since, if there are other stable points, the Lyapunov function will also obey relation (7) in the neighborhood of these points. The Lyapunov function is like a topographic surface with peaks, valleys, pits, and saddles. The stable points are at the pits, which are local minima of W. Unstable points are peaks of the Lyapunov surface, and the system will move away from these peaks toward lower values of W.

For ecology the problem of Lyapunov functions is to what extent they represent interesting biological statements. To say that a physical system moves to a state of minimum poential energy gives an insight into the workings of the physical universe. It somehow increases one's "understanding," by providing a unifying concept for a diversity of systems. What is the equivalent ecological law? What is minimized during succession? Will it be a useful and illuminating quantity or simply a mathematical formalism with no intuitive content? MacArthur[5] has recently defined a quantity that is minimized in a purely competitive situation. No general solution in ecological terms has yet been given. An example of a mathematical form is

$$W(n)=\sum_{i}(1-|\lambda_i|^2)\,|y_i(n)|^2 \qquad (8)$$

where the λ_i are the eigenvalues of **L** [see Eq. (5)] and the $y_i(n)$ are the associated orthogonal deviations from equilibrium, calculated from the x_i.

BOUNDED SYSTEMS

In the discussion of global stability it was pointed out that whether or not a locally stable point was also globally stable depended in part on whether points for which some components are zero are considered. In a biological context, the value zero (or infinity) has a special meaning. The presence or absence of species is sometimes the point of interest regardless of some variation in their numbers or relative abundance from time to time. In the n-dimensional space used for describing the state of a system we will distinguish between *interior points* and *boundary points*. The boundary set will include all points for which one or more of the vector components is zero, but may also include some other points. For example, if the number of tree holes suitable for tree swallow nests in an area is K, we may wish to consider K as a boundary for the number of nesting pairs of the swallows and ask whether the number of adult females is always less than K. The boundary set is defined by the problem. We will say that a system is *dynamically bounded* in some interior set S if at all points in the neighborhood of the boundary set B the transformation vectors point into the interior set S. That is, *no point in the boundary set is stable*. For example, let us take the problem of invasion. Zero abundance for any species is an equilibrium, since once the number gets to zero it will not change. Yet the structure of the community may be such that if one pair of individuals of this species were introduced the numbers would then rise. Thus the boundary value, although an equilibrium, is not a *stable* equilibrium, and we will say that the community is *dynamically bounded* away from zero for this species. Only some random external force could eliminate the species, and if it were reintroduced it would increase. It is important to note that to be dynamically bounded does *not* imply that some interior point is stable! It is entirely possible for no particular interior point to be stable, yet for the system to be always kept away from the edges. For example, if the environment varies randomly in such a way that one species is favored on the average but a second species is very strongly favored in occasional years, there will be no stable equilibrium abundance of the two species relative to each other, but neither species will ever be eliminated.

RELATIVE STABILITY

The concepts of local and global stability are absolute. Either a point is locally or globally stable or it is not. This does not distinguish *degrees of stability*, although such relative stability has important biological content. To understand relative stability we must return to the Lyapunov function and the basin of attraction of a stable point. If there are multiple stable points for a system, they may differ in the conformation of their domains of attraction. One stable point might have a very small basin of attraction, but the gradient of the W function might be very steep in the neighborhood of the point. Indeed the basin of attraction might itself lie at the top of a steep *upward* gradient of W. Such a region would resemble a volcano with a crater at its summit. The center of the crater is a stable point but an unlikely one for any system because its domain of attraction is small and it is surrounded by regions of large W. However, if the system should by chance get into the basin of attraction, it would very rapidly evolve into the potential well with its steep sides and, once in that basin, would be held very strongly.

By contrast we may consider a stable equilibrium point with a very large domain of attraction but with a very shallow gradient in its W function. Thus the system is very likely to fall into this domain, but will move very slowly toward the equilibrium and can be easily perturbed from it. The depth of the potential well can be easily quantified as the difference between the values of W at the equilibrium and at the edges of the basin. Indeed a general index of shape is the ratio of the depth to the radius of the basin. Setting the subscript 0 to stand for equilibrium and the subscript B to stand for a boundary point of the basin of attraction, a shape index would be

$$I = \sqrt{\sum_i (v_{i0} - v_{iB})^2} \Big/ (W_B - W_0) . \tag{9}$$

Small values of I would indicate small deep regions of stability, large values denoting large shallow ones.

A third aspect of relative stability is in the shape of the basin of attraction along the various dimensions of the state space. The basin need not be circular (hyperspherical) in cross section. There may be great stability to perturbation in some directions but little stability in others. The eigenvalues of the matrix **L** give a measure of this shape in the neighborhood of the equilibrium. The rate of change of position along each dimension of the hyperspace is a linear function of the eigenvalues. By a suitable transformation of axes the space may be represented along a set of orthogonal axes each associated with one of the eigenvalues. The stability of the equilibrium with respect to each of these axes is then directly measured by its associated eigenvalue. Eigenvalues close to unity correspond to weak stability in the sense that a perturbation along an associated orthogonal dimension will result in a very slow return to equilibrium along that axis. An eigenvalue close to zero on the other hand means a high stability and rapid return.

A fourth measure of relative stability arises when we consider larger deviations from equilibrium. Since the rate of change of position along each dimension is a function of all the eigenvalues even in a linear system, it may be strongly dominated by the imaginary parts of some complex eigenvalues when the position is far from equilibrium. This means that there will be oscillation, with the system taking a spirally winding path inward toward the equilibrium, with very long time periods and an apparently erratic behavior. Oscillatory phenomena have received a great deal of attention in ecology, but usually the search is for some driver of the oscillation rather than for internal mechanisms intrinsic to the dynamical system itself. Part of the problem of relative stability is whether the complex eigenvalues play an important role far from equilibrium. Somehow we judge a system to be more stable if the oscillatory component is weaker, and this, in turn, is a question of the relative sizes of the eigenvalues.

Once again, for nonlinear systems the eigenvalue approach breaks down when the system is far from equilibrium, and stability theory of nonlinear processes is poorly developed.

STATISTICAL ENSEMBLES

The problem of relative stability discussed above is important because we believe the world of real objects to be subject to a host of random perturbations, random at least with respect to the dynamical system we have specified. I do not wish to go here into the question of the ontological status of random events. It is sufficient to say that any predictive system that can be managed practically will have variables that must be considered as extrinsic to the system and random with respect to it. Since the state of the system is being perturbed, it will never be exactly at any equilibrium point or in any equilibrium cycle. Rather, its position will be determined by a combination of random perturbations on the one hand and a restoring force, expressed by the Lyapunov function, on the other. Through time the system will occupy a series of points in the hyperspace, and the ensemble of those points will form a cloud around the stable equilibrium position. This time ensemble is really an expression of the probability density of the system in n-space. The density of the cloud will follow the shape of the relative stability measures previously discussed. If I is large, the cloud will be very dense around the stable point but will be of small radius. The density can be decreased and the radius increased for this very same equilibrium point by increasing the size of the random perturbations. When I is small, the cloud will be large and diffuse, but again it may be less so if the perturbations are smaller. It is useful to think of the "temperature" of the ensemble measuring the mean square distance of points in the ensemble from the average (not necessarily the deterministic equilibrium point).

Let $[x]$ again be the vector of deviations from equilibrium for the system. Then, if the transformation of the system is a set of linear equations F, the probability density $p(x)$ at point x is the solution of the Fokker-Planck equation

$$\sum_{i=1}^{n} \frac{\partial}{\partial x_i}(F_i p) - \frac{1}{2}\sum_{i,j=1}^{n} \frac{\partial^2}{\partial x_i \partial x_j}(d_{ij} p) = 0 \tag{10}$$

where d_{ij} is an element in the variance-covariance matrix of the perturbations. This equation has the general solution of the form

$$p(x) = K^{-W} \tag{11}$$

where W again is the Lyapunov function of the system. As we expect, Eq. (11) tells us that the probability density is highest where the Lyapunov function is at a minimum. In fact $-\log p(x)$ has exactly the shape of the Lyapunov function itself. The constant K is a function of the variance-covariance structure of the random perturbations.

This general theory has been applied by Kerner[7] to the specific case of a prey-predator community, and he derived an expression of the general form of (11). Kerner calls attention to the parallel with the Gibbs ensemble of statistical mechanics and especially to the notion of "temperature." If we define the "temperature" of the ensemble as the mean square distance of points in the ensemble from their mean position in the hyperspace, then we have a descriptive parameter expressing the cloud density and the tendency to remain near the equilibrium point. As "temperature" is defined, it is, in fact, the variance of the probability density function.

CONSTANCY AND STABILITY

The notion of the equilibrium ensemble of position vectors points up the important difference between constancy and stability. Constancy is a property of the actual system of state variables. If the point representing the system is at a fixed position, the system is *constant*. Stability, on the other hand, is a property of the dynamical space in which the system is evolving. Thus, if there is a stable equilibrium point in the vector field, it does not follow that the community must be constant at that point. Because of the random perturbations of the environment or of numbers of organisms in it, the actual state of the system is in constant flux. Yet there is *stability* in the dynamical sense because the ensemble of state points of the system maintains a steady state distribution with its center near a stable point of the deterministic dynamical system and with a constant "temperature" determined by the statistical properties of the random perturbations.

STRUCTURAL STABILITY

The vector field of transformation vectors is determined by the laws of transformation of the quantities defining the dynamical space. There will be a certain number of stable equilibria, unstable points, and perhaps limit cycles. We may now ask what would happen to the vector field if a very small change were made in the parameters of the equations determining the transformation. If the set of equations defining the system is "well behaved" in some sense, a very small change in parameters will make a very small change in the configuration of the vector field. The locations of the various stationary points or limit cycles may change slightly and the values of the Lyapunov function very slightly at each point of the space. But nothing catastrophic will occur, and the difference will hardly be noticed. If we regard the equations T as mapping the parameter space into the space of equilibrium points, then neighborhoods map into neighborhoods, infinitesimal changes in one space causing only infinitesimal changes in the other. On the other hand the laws of transformation may be very badly behaved so that a small change in parameters completely alters the kind of vector space produced. Neighborhoods of the parameter space do not map into neighborhoods of equilibrium space. Such a system is said to be *structurally unstable*. The Lotka-Volterra model of prey-predator interaction is an example of a structurally unstable system. In the simplest model there is no self-damping term, and the numbers of prey (N_1) and predator (N_2) change in time according to the equations

$$dN_1/dt = r_1N_1 - kN_1N_2; \quad dN_2/dt = KN_1N_2 - d_2N_2, \tag{12}$$

where r and d are the birth and death rates of the prey and predator, respectively, and the k's are species interaction constants. As is well known, the solution to these equations is set of closed curves in the N_1N_2 plane so that there is a perpetual undamped oscillation of prey and predator. If, however, second-order terms are added in N_1 and N_2 which introduce self-limitation, the closed curves in the N_1N_2 plane break open and become spirally winding paths leading to a stable point. Thus an infinitesimal change in the coefficients of the higher-order terms (from zero to nonzero) causes a radical alteration in the outcome of the species interaction. Several cases are known in population genetics.

The existence of such structural instabilities is very disquieting, since it means that predictions are very sensitive to assumptions. This makes an adequate predictive theory of ecology very difficult, and it must be hoped that such structural instabilities will prove to be the exception.

STABILITY AND HISTORY

A stable point or a stable limit cycle is one toward which all the neighboring vectors point. It is then a point that will be reached from any direction. If a community is at such a stable point, it is impossible to say from which direction in the hyperspace it came. Thus, historical information is destroyed at equilibrium. All is not lost, however, since at least we know that the community began in the basin of attraction of the particular equilibrium point. On the other hand, if the system is at a transient point, it is possible to reconstruct both its past and its future, since one and only one trajectory passes through each transient point in a space of sufficient dimension.

In population biology there are often two opposing modes of explanation. The first states that history is relevant to the present state of populations, species, and communities, and that their present state cannot be adequately explained without reference to specific historical events. This is equivalent to saying that multiple stable points exist and that the interesting problem is why the system is at a *particular* stable point, or else to claiming that the system is at a transient point. The second mode of explanation attempts to explain the present state of natural populations or communities without any historical information, but as a result of certain fixed forces.

This mode is equivalent to saying that the system under study is at a point of global stability, or else is one point in a stationary ensemble of points, removed from a globally stable point only because of small random perturbations. The first mode of explanation concentrates on the particular community and its trajectory in the dynamical space, while the second concentrates on properties of the dynamical space alone. However, only its equilibrium properties can be deduced in this way. If the general configuration of the dynamical space is to be discovered, that is, if the dynamical laws governing the transformation and evolution of communities are to be discovered, it is essential to work with non-equilibrium systems through time either by a search for evolving communities or by a deliberate perturbation analysis of communities at present at stable points.

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DISCUSSION

Watt: Richard Bellman, one of the world's leading experts on the stability theory of systems of differential equations, has recently written a book arguing that this body of theory is inappropriate for dynamically controlled systems, as opposed to systems where "control" is merely built into the design at the outset. I wonder if you would agree or disagree with him.

Lewontin: I tried to argue that the classical theory of neighborhood stability is, indeed, inappropriate, if that is what Bellman is arguing. I say that the classical theory of neighborhood stability, the theory expounded in Bellman's book – the conditions of eigenvalues of the linearized transformation – is inappropriate for two reasons. One is that it reveals nothing about global stability, which is of interest for ecological purposes. But more important, it is not a theory that leads directly to the description of a probability density cloud, the sort of Gibbs ensemble which is much more interesting in ecology. We need a theory much more closely allied to statistical mechanics, with some dissipation. We are really dealing with a kinetic theory of gases but with imperfectly distributed gases, and I agree entirely that the description of the local stable points is only the beginning.

Watt: You are saying what Bellman is saying, but I wonder where he is leading us, and whether statistical mechanics is the answer. It seems that statistical mechanics is based on assumptions that don't match the realities.

Lewontin: I am not talking about statistical mechanics which assumes a conserved quantity, which assumes perfect elastic collision. I am talking about a system in which we describe the dissipation of the population, its going toward some stable point, and compensate for it by perturbations – in fact, theory of diffusion process. I have written a Fokker-Planck equation that contains this dissipation in it and which, when solved, will give a description of the probability distribution of points in n-dimensional space. If you ask me how probable it is that communities will have 7 of one species, 14 of another, 209 of a third, and so on, I can answer that, if you tell me two things: (a) what is the configuration of the dynamical space as far as its deterministic elements are concerned, and (b) how much random perturbation goes on. That is what is done in genetics when we determine the probability of gene frequencies over an ensemble of populations from the rules of deterministic transformation by which gene frequencies are being forced by natural selection and the rules of random variation. One puts these together in a diffusion equation or some kind of a more exact description of a Markov process, and comes up with a probability distribution. I think that is the appropriate mathematics for community ecology.

WATT: Doesn't the Fokker-Planck equation involve implicit assumptions about the statistical character of exogenous perturbations operating on the system that don't correspond to what happens in nature?

LEWONTIN: I don't know whether they correspond or not, and the difference between you and me is that you are used to thinking very exactly about very exact situations. I don't consider the Fokker-Planck to be a perfect equation. Statistical perturbation theory is the appropriate theory, and, if the Fokker-Planck equation is inappropriate because the process is not Markovian, or because it does not satisfy the proper rules about the higher moments, then we have to set up some other equation. The Fokker-Planck equation is derived by neglecting the higher moments. If we can't neglect them, we need a bigger equation, which is more difficult to solve.

WATT: I am still trying to find out what the theory has to be and I mentioned the Fokker-Planck as an example. I am sure the Fokker-Planck equation itself is a wrong equation.

FOSBERG: You discussed three types of points. Which of them is represented by a dynamic equilibrium that, although it revolves about a stable point, does not necessarily return to that original point? The situation you described seemed to involve a return to the original point.

LEWONTIN: No, it doesn't. In the second half of my talk I tried to show that any real biological system does not get back to the equilibrium point because of the perturbations. I am trying to arrive at a description of the system by building up from a deterministic system which has such stable points. If there were no further perturbations, it would finally go back to such points The real biological system, the community, is moving in such a potential field, but it is always being knocked out by some other forces; or, if you like, you can regard this particular vector field with its stable point as only one of a series of vector fields, each of which is applicable at a given instant of time. So, you never return to any particular stationary point. The stationary point is the center of the cloud of probability. It is exactly like taking a pingpong ball in a bowl, and wiggling the bowl constantly – the ball is always moving around yet you can still describe the system as a potential well plus random perturbations.